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Initial observations on this subject were presented at the Thirteenth Western States Sage Grouse Workshop, Ontario, Oregon, August 30 - September 1, 1983, under the title "Evidence of a Ten-Year Population Cycle in Sage Grouse." After considerable more analysis of the subject, Mr. Rich presented information from this bulletin at the Idaho BLM Wildlife Workshop, Boise, Idaho, March 4-6, 1985. He also has submitted this information to the journal *The Auk* for formal publication.

After mid-April 1985, Mr. Rich's duty station will be U.S. Bureau of Land Management, Dickinson District Office, Dickinson, North Dakota 58602.

SAGE GROUSE POPULATION FLUCTUATIONS: EVIDENCE FOR A 10-YEAR CYCLE

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ABSTRACT.-Thirty-two years of counts of Sage Grouse (Centrocercus urophasianus) males on leks in southern Idaho revealed major population peaks about every 10 years. Lek counts from northern Utah and western Nevada and harvest data from Idaho and Utah all show strong synchrony in this cycle. Individual lek counts within each region tended to fluctuate together despite being located in different habitats or at different elevations. Eight of nine monthly weather variables having significant correlations with lek counts in Idaho were precipitation, rather than temperature, variables. However, weather variables were not useful in predicting mean lek counts through linear-regression analysis. In Idaho 79% of the variation in mean lek count could be explained by knowing the mean lek count of the previous spring and the juvenile/adult ratio in the preceding autumn's harvest. About 65% of the variance in the juvenile/adult ratio could, in turn, be explained by knowing the amount of precipitation in July and August. There is no evidence that Sage Grouse populations decline as a result of being alternate prey in a predator-prey system involving coyotes (Canis latrans) and cycling black-tailed jackrabbit (Lepus californicus) populations.

In this paper I propose to test the hypothesis that Sage Grouse (Centrocercus urophaisnus) populations in three western states are oscillating together annually and that their oscillations are similar to the well-known 10-year cycle of the boreal forest of Canada (Keith 1963, Bulmer 1974, Finerty 1980). Such a population cyclicity in the Sage Grouse was suspected by Patterson (1952) but no data analysis was presented. I further examine several weather and population variables through multiple linear-regression analysis in order to identify variables that might be useful in a population model for this species.

Currently among the tetraonids, evidence for a 10-year population cycle exists for the territorial Willow Ptarmigan (Lagopus lagopus) (Bergerud 1970, 1971), Rock Ptarmigan (L. mutus) (Gudmundsson 1960, 1972; Weeden and Theberge 1972), and Ruffed Grouse (Bonasa umbellus) (Bump et al. 1947, Keith 1963). Less evidence is available for the lekking Sharp-tailed Grouse (Tympanuchus phasianellus) and Greater Prairie-chicken (T. cupido) (Hamerstrom and Hamerstrom 1954, Lack 1954, Williams 1954, Keith 1963). The Sage Grouse is a lekking species.

METHODS

Male Sage Grouse have been counted on leks by a number of biologists over the years, including the author, on 24 leks in southern Idaho, 9 leks in northern Utah, and 6 leks in western Nevada (Fig. 1). Data from these leks were selected from among a greater number of known leks in historical files on the basis of having at least seven, and up to 32, consecutive years of lek counts (Table 1). In Idaho, about 2 (range 1 to 7) counts of males were made per lek per year. In Utah, about 3 (range 1 to 5) counts were made per lek per year since 1978. Before that, at least 2 counts were made in most cases. In Nevada, about 1 count was made per lek per year. Where more than 1 count was made in a given spring, I used the maximum number of males in analysis. Female counts were available for many dates, but these counts are less reliable due to the female's much smaller size and inconspicuous behavior. Therefore, no female count data were analyzed.

Harvest data for Idaho consisted of the total kill on the opening weekend of hunting season from the following harvest units of the Idaho Department of Fish and Game: North Shoshone-Burma-Richfield, East Fairfield, and North Gooding. I present similar data from Box Elder County, Utah and Washoe County, Nevada.

Weather data were only examined for Idaho and were taken from the nearest appropriate weather station of the National Oceanic and Atmospheric Administration (Fig. 1). Weather variables consisted of mean monthly precipitation and mean monthly temperature for December through June between 1951 and 1982. I analyzed weather effects for subsets of leks (Table 1) that were grouped in the same habitat, were near one another and a weather station, and had relatively many years of lek counts. For the Picabo Hills lek complex, I used the average values of weather variables for Picabo and Richfield. Data were available from Richfield since 1951, but those for Picabo between 1951 and 1959 had to be estimated. A separate linear regression was established for each month using temperature and precipitation at Richfield between 1960 and 1982 as the predictor variables. The $\underline{r}^2$ values for these regressions were between 0.79 and 0.94 (all $\underline{P} < 0.001$). For the North Laidlaw lek complex I used the average values of weather variables from Richfield and Craters of the Moon. Weather data for Craters of the Moon between 1951 and 1959 were estimated from Richfield data as described above. Weather data for the South Laidlaw lek complex were taken from Richfield and those for the Bennett Hills complex were from Hill City.

In the discussion of multiple regression I use several abbreviations to shorten the text. Weather variables are given as the first three letters of the month followed by a "P" for precipitation or "T" for temperature. The mean maximum number of males on a lek is represented by "Lek" and the juvenile/adult ratio in the opening weekend of harvest by "Juv/Ad". For all variables the subscript "$_t$" refers to the subject year and "$_{t-1}$" to the previous year.

Stepwise multiple regression, missing value correlation, and spectral analysis were computed with programs in the BMDP series (Dixon 1981). Mean lek counts were generally proportional to their variances, so in linear-regression analysis I analyzed both the raw data and the raw counts sqare-root transformed. Spectral analysis was performed on log-transformed data (Finerty 1980). All weater data were normally distributed. Because Lek_t and Lek_{t-1} were not independent, all P values involving these variables are for general guidance and should not be taken at face value.

RESULTS

LEK SIZES AND HABITATS

The mean maximum count of males by lek over all years ranged from 10.6 at Warm Springs Road to 110.4 at Nolan Ranch (Table 1). Among the ten lek complexes and their associated nesting habitats, five were dominated by different species or subspecies of sagebrush (Artemisia sp.) (Table 1). Although the Picabo Hills and South Laidlaw were both dominated by Wyoming big sagebrush (A. tridentata wyomingensis), the latter lek complex averaged 100 m lower in elevation, 3 cm less yearly precipitation, and 0.6° C greater mean annual temperature. These factors contribute to the two sites being different habitats, e.g., the dominant grass in the Picabo Hill was bluebunch wheatgrass (Agropyron spicatum) whereas that in South Laidlaw was cheatgrass (Bromus tectorum). In Utah, the Dove Creek and Rosebud complexes were in similar black sagebrush (*A. nova*) habitats (Table 1), but the mean elevations differed. In Nevada, all leks were in *A. arbuscula* habitats, but again the mean elevations of the lek complexes were different. Generally, the leks reported here were located in different combinations of nesting habitat and elevation, and, hence, precipitation and temperature.

POPULATION FLUCTUATIONS

Idaho.--The mean maximum number of males on the 24 Idaho leks peaked in 1955 or 1958, 1970, and 1980 and reached lows in 1964, 1976, and, possibly, 1982 (Fig. 2). There was a mean of 70.7 males on the 19 leks counted in 1970, the highest population year, and a mean of 15.7 males on the 14 leks counted in 1982, the lowest year to date.

The individual lek counts tended to fluctuate in synchrony with each other. Of the 276 possible pairwise correlations among the counts on 24 leks, 215 correlations were positive and 61 were negative. Among the positive correlations, 97 were significant at $P < 0.05$ including 35 at P 0.001. This contrasts sharply with the negative correlations where only seven were significant at $P < 0.05$ including one at $P < 0.01$. A similar correlation matrix from random numbers would be half negative and half positive with only about 14 correlations significant at $P < 0.05$.

Spectral analysis of these data shows that the sine wave making the largest contribution to the Idaho population curve has a period of 0.10 cycles/year or 1 cycle/10 years (Fig. 3). There is also a large contribution from a wave with a period of 0.12 cycles/year or 1 cycle/8.3 years.

Total opening-weekend harvest since 1962, although subject to sundry confounding variables, coincided with the lek-count data. Peak harvests occurred in 1971 and 1980 with lows in 1965 and 1975 (Fig. 4). The total opening-weekend harvest was significantly correlated with mean maximum lek count of the same year ($r = 0.63$, $P < 0.005$).

Utah.--The mean maximum number of males on nine leks in Utah peaked in 1969 and 1980 and possibly 1959 and reached lows in 1964 and 1974 (Fig. 2). The highest number was reached in 1980 with a mean maximum of 72.7 males on nine leks. The low was 17.5 males on two leks in 1964.

The synchrony of Utah lek counts was not as marked as that for Idaho but, nevertheless, lek counts did fluctuate together. Of 36 possible pairwise correlations between counts, 24 were positive and 12 negative. Seven of the positive correlations were significant at P 0.05 (four at $P < 0.001$) whereas none of the negative correlations was significant.

Spectral analysis of these data revealed a peak at 0.12 cycles/year or 1 cycle/8.3 years (Fig. 3). The contribution of a sine wave with 1 cycle/10 years was relatively great but no more so than that of a wave with 1 cycle/6.3 years.

Total opening-weekend harvest since 1969 peaked in 1970 and 1979 with a low in 1975 (Fig. 4). As in Idaho, harvest data were significantly correlated with the lek counts ($r = 0.64$, $P < 0.02$).

Nevada.--Lek counts for western Nevada are available for a shorter period of time and show a peak in 1979 with possible lows in 1975 and 1983 (Fig. 2). Again, leks tended to fluctuate together. Of 15 pairwise correlations between lek counts, 12 were positive and 3 negative. Five of the positive correlations were significant at P 0.05 (two at $P < 0.001$) and none of the negative correlations was significant. These data were insufficient for spectral analysis.

Harvest data from Washoe County does not broadly coincide with harvest data for Utah and Idaho and does not suggest a 10-year cycle (Fig. 4). This is chiefly because of the large number of grouse harvested in 1973 and 1974. Lek counts and harvest data were similar to each other from 1976 to

1982. Also, the low in the Washoe County harvest in 1976 and peaks around 1970 and 1980 were similar to those in Idaho and Utah (Fig.4).

MEAN LEK SIZE IN IDAHO

Weather Variables.--Stepwise multiple-linear regression of weather and population variables revealed that using Lek_t or Lek_t square-root transformed produced nearly the same results. Therefore, I will only discuss the results of analysis with the untransformed data.

For all Idaho data combined, three weather variables were significantly correlated with Lek_t (Table 2), but each explained less than 5% of the variation in Lek_t. In the multiple regression, only Lek_{t-1} was entered. The significance of this regression is undefined because Lek_t and Lek_{t-1} are not independent. However, 53% of the variance in Lek_t was explained and the P value (< 0.001) point out the strong serial relationship.

Because each of the lek complexes in Idaho was in a different combination of habitat and climate, it is useful to examine each lek complex separately. In the Picabo Hills two weather variables had significant correlations with Lek_t but only Lek_{t-1} was entered into the regression (Table 2). This is the only complex where a June variable was significantly correlated with Lek_t.

In South Laidlaw, two weather variables were significantly correlated with Lek_t but only Lek_{t-1} was entered into the regression (Table 2). In South Laidlaw, the Picabo Hills, and for the total data set, there was a positive correlation between Lek_t and January precipitation of the same year. This was the second most consistent pattern among the correlations.

In North Laidlaw, no weather variables were significantly correlated with Lek_t (Table 2). However, Lek_{t-1} was highly correlated and was entered into the regression.

The Bennett Hills complex was unique in that Lek_{t-1} was not significantly correlated with Lek_t, and no variable was entered into the regression (Table 2). It is also the only case in which a temperature variable was significantly correlated with Lek_t.

In summary, although weather variables showed some significant correlations with population size, none of them was useful in predicting population size. Knowledge of the previous year's population size, however, was useful in prediction in all cases but the Bennett Hills.

Age Ratios.--One other data set available for prediction of Lek_t was the juvenile/adult ratio in the harvest. Because the harvest data cover a general geographic region, the dependent variable must be a yearly mean for all leks by state, i.e., the lek complexes cannot be analyzed separately. Two relationships with Juv/Ad were examined: That between the subject year's lek count and following autumn's age ratio (Lek_t and Juv/Ad_t) and that between the subject year's lek count and the previous autumn's age ratio (Lek_t and Juv/Ad_{t-1}).

In all three states there was no significant linear regression with Lek_t as the independent variable and Juv/Ad_t as the dependent variable (Idaho, $r^2 = 0.06$, $0.20 < P < 0.50$; Utah, $r^2 = 0.03$, $0.50 < P$; Nevada, $r^2 = 0.13$, $0.20 < P < 0.50$). However, Juv/Ad_{t-1} did explain a significant amount of the variation in Lek_t in Idaho (Fig. 5). In Utah and Nevada there was no relationship ($r^2 = 0.00$, $0.50 < P$ and $r^2 = 0.05$, $0.50 < P$, respectively).

The age ratio also improved the prediction of Lek_t when entered into the multiple linear regression with variable Lek_{t-1} for Idaho ($Lek_t = -6.8 + 10.0\ Juv/Ad_{t-1} + 0.7\ Lek_{t-1}$, $R^2 = 0.79$). As before, Lek_t and Lek_{t-1} are not independent and the P value (<0.001) is only suggestive of a strong relationship. Thus, 79% of the variation in mean maximum lek size of 24 leks in Idaho between 1962 and 1983 can be explained by knowing the previous year's mean lek size and the juvenile/adult ratio of the previous autumn's opening-weekend harvest.

Because there was no significant relationship between mean lek count and the following autumn's age ratio, I examined summer precipitation variables in an attempt to explain some of the variation in that age ratio. A highly significant linear regression was obtained with August precipitation accounting for 51% of the variation in Juv/Ad_t (Fig. 6). Summers with unusually high August precipitation tend to lead to higher proportions of juveniles in the fall harvest. The relationship was not well defined in years of low precipitation, however, as two years with no August precipitation were still followed by relatively high proportions of juveniles (Fig. 6). Also confusing the interpretation somewhat was the fact that July precipitation had a significant negative correlation with Juv/Ad_t ($\underline{r} = -0.48$, $\underline{P} < 0.05$). This variable also significantly improved the linear regression ($Juv/Ad_t = 1.4\ -0.2\ JulP_t + 0.2\ AugP_t$, $\underline{R}^2 = 0.65$, $\underline{F} = 16.77$, $\underline{P} < 0.001$). Although no weather variables were examined for Utah, the age ratios in Idaho and Utah were correlated ($\underline{r} = 0.72$, $\underline{P} < 0.005$). This suggests that whatever factors influenced survival of juvenile Sage Grouse over the summer period may be operating in the same way in the two states. There was no significant correlation between the age ratios of Idaho and Nevada ($\underline{r} = 0.17$, $0.50\ \ \underline{P}$) or Nevada and Utah ($\underline{r} = 0.32$, $0.20\ \ \underline{P} > 0.50$).

DISCUSSION

The evidence presented suggests that Sage Grouse populations might be undergoing a 10-year cycle. Patterson (1952, p. 35) thought it was ". . .

highly probable that this species of grouse may also be exhibiting the cyclic phenomena or oscillations so well associated with most other grouse and upland game birds." Patterson (1952) did not pursue his thinking with analysis of his Wyoming data but did cite evidence of population peaks in 1931-33, 1941, and 1950 with lows in 1935-37 and 1945-47. If this pattern in Wyoming were extended, it would coincide with the cycles reported here. Other historic information on Sage Grouse population cycles is sketchy at best. A marked population drop in 1932 in Utah was thought to be a result of cyclical fluctuations induced by parasites (Stoddard and Kay, unpubl. report in Lords 1951). Hamerstrom and Hamerstrom (1961) stated that the Sage Grouse had undergone dramatic, but poorly understood, changes in abundance.

Other ecological information for Sage Grouse is consistent with certain features of species wherein some populations are cyclic. The sagebrush steppe habitat is relatively simple (Dasmann 1964, Bendell 1972), the habitat occurs in large continuous blocks (Fig. 1, Leopold 1933), winters are cold and snowy, and the winter diet is simple (Patterson 1952, Wallestad 1975, Watson and Moss 1979). In addition, population fluctuations are often greater in marginal habitat (Rowan 1948, Hildén 1965, Jenkins et al. 1967, Linden and Rajala 1981). Sage Grouse habitat in southern Idaho, with which I am most familiar, is clearly inferior to that in the higher elevations of Idaho and Colorado in having less annual precipitation and a depauperate herbaceous flora (pers. obs.). Both vegetative and insect food resources are apt to be less available, particularly in summer (see below).

Keith (1963) pointed to a major problem with Cole's (1951, 1954) hypothesis that cycles can be generated by random fluctuations. Namely, it is difficult to explain repeated snychrony of populations in different regions and habitats. Yet both the lek count and harvest data for Sage

Grouse show marked synchrony of populations in several different habitat types separated geographically by considerable distances. The differences in habitat types are important to Sage Grouse because the stature and palatability of the different sagebrush taxa and, hence, their suitability for food, nesting, and winter cover, varies considerably (Winward 1970, Autenrieth 1981). One must, therefore, examine possible explanations for cyclicity that go beyond local vegetation dynamics.

The attempt to discover the population-control mechanisms in cycling grouse is a complex undertaking (Bump et al. 1947, Cole 1954, Jenkins et al. 1967, Myrberget 1972, Weeden and Theberge 1972, Watson and Moss 1979). The analysis of weather data was presented here despite the fact that weather, as a sufficient cause for cyclical populations, has been widely discredited and may, most importantly, synchronize regional fluctuations (Lack 1954, Bergerud 1970, Bendell 1972a, Myrberget 1972, Watson and Moss 1979). It is possible that such a synchronization has caused the Idaho and Utah data presented here to be more similar to each other than either is to the Nevada data. Unfortunately, the sample sizes for Nevada lek counts are relatively small and the harvest data somewhat incomplete. It is probably unwise to attempt too much explanation for patterns there.

Even if inadequate to cause cycles, the Idaho weather data do suggest some biologically meaningful relationships that should be considered in a population model for the species. These data are consistent with the finding that chick mortality due to wet weather during the brood-rearing period is not sufficient to account for following-year population size (Jenkins et al. 1967, Bergerud 1970, Bendell 1972a, Myrberget 1972, Watson and Moss 1979). Because most Sage Grouse chicks are hatching in April, May, and June (R. Autenrieth, pers. comm.), I had expected the weather variables during these months to emerge with more significant correlations. However, only one weather variable during the brood-rearing period, $JunP_{t-1}$, was correlated with Lek_t and that positively in the Picabo Hills complex. June precipitation may have caused a greater production of insects (Potts 1972) for young Sage Grouse and, thus, had a positive rather than a negative effect.

Eight of the nine weather variables having significant correlations with Lek_t involved precipitation, not temperature. In a region where precipitation is low and variable, it is not surprising that the amount and timing of that precipitation may affect grouse populations. The only significant correlation between Lek_t and a temperature variable was in the Bennett Hills where a positive correlation existed for $DecT_{t-1}$ and Lek_t. This may be biologically meaningful in that this lek complex is substantially higher than the other three (Table 1). Perhaps this is the one area where winter temperatures do become severe enough to affect survival. This was also the only area showing a relatively large negative correlation between a winter precipitation variable and Lek_t.

It has generally been assumed that fluctuations in grouse populations are in some way related to chick production and survival even if an extrinsic factor such as spring weather is not the ultimate casual factor (Bump et al. 1947, Hoffman 1958, Bergerud 1970, Myrberget 1972, Redfield 1975, Watson and Moss 1979). An intrinsic factor to consider is how production varies with breeding bird density. The juvenile/adult ratio for Idaho, Utah, and Nevada populations showed no significant linear relationship with population size of the preceding spring. Jenkins et al. (1967) also found no relationship between breeding success and population density of Willow Ptarmigan. In one case, the percentage of juvenile Willow Ptarmigan in autumn was actually negatively correlated with the size of the nesting population (Myrberget 1972). A similar observation has been made for Ruffed Grouse (Bump et al. 1947). Conversely, in another subspecies of the Willow Ptarmigan, there was greater chick survival during population increases than during decreases (Bergerud 1970).

Although the juvenile/adult ratio was not significantly correlated with the preceding spring's population level in Sage Grouse, that ratio was positively correlated with the following spring's population level. This situation suggests that juvenile mortality over the summer period is more variable than over the winter. Constant mortality over winter has been reported for both Willow Ptarmigan (Bergerud 1970, Myrberget 1972) and Rock Ptarmigan (Weeden and Theberge 1972).

The effect of relatively great August precipitation on the proportion of juveniles in the fall harvest in this study was striking. Yearly precipitation reaches its low point in southern Idaho in July (0.35 ± 0.35 cm, c.v. = 100%) which is a relatively sharp drop from that in June (1.17 ± 1.03 cm). August precipitation (0.54 ± 0.80 cm, c.v. = 148%) is substantially more variable than that in July. Thus, young birds may be especially susceptible to effects of August precipitation if they are stressed by having just passed through the driest month of the year. The availability of forbs and insects for food undoubtedly varies directly with precipitation. Summer mortality among juveniles may also be largely responsible for declines of Ruffed Grouse and Sharp-tailed Grouse (Keith 1963). It is puzzling, however, that years with no August precipitation may also result in a relatively large proportion of juvenile Sage Grouse in the harvest and that July precipitation was negatively correlated with the juvenile/adult ratio. I have assumed that the number of adults remains more constant over summer than the number of juveniles and that the juvenile/adult ratio is mainly a function of variability in juvenile production and survival. Obviously, adult numbers also vary and the relationship between summer precipitation and survival of both age classes deserves further study.

Although my work did not involve any assessment of the possible effects of predation, information is available for southern Idaho and northern Utah that bears directly on this question. Lack (1954) believed that predator-prey interactions could produce cyclical population fluctuations under certain conditions, especially where there were few alternate prey species for a given predator. If the main prey species was cycling for some reason (e. g., Keith 1983) and began a decline, predators would switch to alternate prey. Because the predator populations had increased with their main prey, they would be at high enough densities to cause a decline in the alternate prey populations, and, thus, a cycle might be induced. If this were the case, oscillations in the alternate prey populations should have a lag of one or two years following oscillations of the main prey (Lack 1954).

In southern Idaho and northern Utah such a predator-prey system involves the black-tailed jackrabbit (*Lepus californicus*) as main prey species, coyote (*Canis latrans*) as main predator (Wagner and Stoddart 1972, Gross et al. 1974, Stoddart 1978, unpubl.), and Sage Grouse as one possible alternate prey species. Jackrabbit populations in the Curlew Valley of northern Utah apparently have had a 10-year cycle since at least 1963 (Fig. 8). This region corresponds with the Utah lek complexes of this paper. Jackrabbit data from the Idaho National Engineering Laboratory (INEL) is closely synchronized with that from Curlew Valley (Fig. 8). Although the INEL data is available for a shorter time period, it suggests that a similar cyclicity is occurring in southern Idaho. Other independent data from southern Idaho support those in Fig. 8. Jackrabbit population peaks have occurred in 1919-1922, 1927, 1936, 1942, 1952, 1958-1960, 1970-1971, and 1981 (J. Harris, pers. comm.).

Stoddart (1978) concluded that the observed jackrabbit cycle in Curlew Valley could be largely accounted for by coyote predation. Given the sharp decline in jackrabbit densities following peaks in 1971 and 1981 (Fig. 8) coyotes would proabably have switched to alternate prey. If Sage Grouse were affected by this system one would expect Sage Grouse populations to have begun declining in 1972 and 1982. Clearly, this was not the case. Sage Grouse populations in all three states peaked at least one year before jackrabbit populations in every instance. Keith (1963) reported that snowshoe hare (Lepus americanus) populations also peak slightly later than grouse, and Hoffman (1958), after reviewing many studies, found that grouse declines frequently precede hare declines. Thus, there is no support for the predator-prey system as outlined by Lack (1954) having induced cycles in Sage Grouse populations. However, the striking synchrony of jackrabbit and Sage Grouse populations in Idaho and Utah certainly calls for explanation. It is not unlikely that predation does play an important role, but the dynamics have yet to be discovered.

The importance of the recognition of a possible 10-year cycle in Sage Grouse lies both in the field of management and research. Evaluations of grouse population responses to habitat changes are critically dependent on understanding the long-term population dynamics of the species, especially where such evaluations may be done over a period of only a few years. In addition, Sage Grouse habitat is often delimited based on the number, size, and locations of leks. Obviously, the years in which leks are located and counted are important. Ten years data may be required to even begin an adequate definition of just the breeding habitat of a population.

The tetraonids as a whole exhibit several behavioral and ecological features that make them attractive subjects for population studies (Bendell 1972b), and I believe the lekking species are even more suitable than the territorial species. In particular, the yearly congregation of male and female Sage Grouse on traditional leks affords several advantages: 1) although the variability in numbers of birds attending a given lek daily in a particular year may be substantial, the major factors influencing attendance are fairly well understood (Jenni and Hartzler 1978). Therefore, lek counts are probably good indicators of population size and trend; 2) the birds are tolerant of vehicles near the lek making not only counts but the study of behavior, which may be important to understanding cycles in grouse (Robel 1972), relatively easy; 3) large blocks of relatively uniform habitat are accessible by vehicle at most times of the year; 4) many lek sites are already documented by wildlife and land management agencies; 5) a large amount of historical data on both Sage Grouse and their habitat, especially wildfire and grazing, is available. Thus, Sage Grouse may be one of the best vertebrate species yet for long-term population studies. This is an especially intriguing situation because black-tailed jackrabbit and coyote populations are also apparently cycling in the same geographic region and much is already known of the dynamics of this predator-prey system.

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Table 1. Habitat and count information for the Sage Grouse lek complexes.

Lek Complex Elevation Habitat	Name of lek	Years of data	Number of Males	
			Mean	SD
Picabo Hills	Wedgetop[a]	30	28.8	29.8
1500 m	Sonner's Reservoir[a]	30	20.1	17.5
Artemisia	Fenced Field[a]	28	45.7	26.4
tridentata	Square Lake[a]	32	31.1	21.1
wyomingensis	Spudpatch[a]	28	77.9	60.1
	LI65	20	33.7	23.7
	LI77	21	51.8	32.0
	Buck Lake	27	25.7	18.1
	Ridge	9	55.9	44.4
Bennett Hills	Fir Grove[a]	24	36.1	25.2
1500 m	Johnson Well [a]	29	55.1	25.7
A. vaseyena	Willow Springs[a]	28	18.7	11.0
	Association Well	23	18.4	16.2
	Ben Dohr Reservoir	25	14.7	11.9
	Hill City Road[b]	17	16.5	10
North Laidlaw	Paddleford Flat[a]	19	27.7	12.1
1500 m	Rock Pile[a]	14	18.5	14.9
A. tripartita	Paddleford No. 1[a]	9	35.8	30.7
	Moran Lake [a]	15	15.9	13.8

Table 1. (Continued)

South Laidlaw	Shale Butte Cabin[a]	29	24.8	23.7
1400 m	Kimama Section 32[a]	30	21.5	17.7
A. t.	Laidlaw Airstrip[a]	31	19.6	13.7
wyomingensis	Steamboat Lake No. 1[a]	30	48.3	40.4
	Beartrap Airstrip	14	35.7	21.1
Dove Creek	Dove Creek	25	71.7	43.4
1700 m	Warm Springs Road	14	10.6	8.5
A. nova	Upper Dove Creek	13	25.9	14.6
Rosebud	Dry Basin	25	84.6	49.4
1750 m	Keg Springs	19	12.1	9.8
A. nova	Badger Flat[c]	21	28.2	16.9
Hardister Creek	Hardister Creek Road	15	34.4	19.5
1800 m	Meadow Creek Pass	14	16.7	6.8
A. arbuscula	Red Bank Springs	15	34.1	26.5
Wall Canyon	Nolan Ranch	8	110.4	31
1800 m	Nolan Sattelite Ground	7	24.4	19
A. arbuscula	Wall Canyon Seeding	8	24.8	20.6
Grass Valley	Clover Creek	9	28.0	14.5
1725 m	Cherry Ridge	9	12.8	6.9
A. arbuscula				

Table 1. (Continued)

Squaw Valley	Squaw Valley	7	42.6	17.8
1700 m				
A. arbuscula				

[a] Idaho leks used in correlation and regression analysis.

[b] Habitat is *A. t. wyomingensis*.

[c] Lek was grouped somewhat arbitrarily with Rosebud.

Table 2. Significant correlations between the criterion variable, Lek_t, and predictor variables for Idaho data. Linear-regression equations are also given.

Lek Complex	*n*	Predictor Variable	*r*	*P*[a]
All Combined	94	Lek_{t-1}	0.73	< 0.001
		$JanP_t$	0.22	< 0.05
		$MarP_{t-1}$	-0.22	< 0.05
		$FebP_t$	-0.21	< 0.05
$Lek_t = 7.5 + 0.7\ Lek_{t-1}$ ($r^2 = 0.53$)				< 0.001
Picabo Hills	28	Lek_{t-1}	0.67	< 0.001
		$JunP_{t-1}$	0.43	< 0.05
		$JanP_{t-1}$	0.39	< 0.05
$Lek_t = 12.9 + 0.7\ Lek_{t-1}$ ($r^2 = 0.45$)				< 0.001
South Laidlaw	28	Lek_{t-1}	0.75	< 0.001
		$JanP_t$	0.47	< 0.02
		$MarP_{t-1}$	-0.44	< 0.02
$Lek_t = 5.6 + 0.8\ Lek_{t-1}$ ($r^2 = 0.56$)				< 0.001
Bennett Hills	24	$DecT_t$	0.57	< 0.005
		$DecP_t$	-0.51	< 0.02
(No variables entered into regression)				

Table 2. (Continued).

North Laidlaw	14	Lek_{t-1}	0.90	<0.001
$Lek_t = 1.8 + 0.8\ Lek_{t-1}$ ($\underline{r}^2 = 0.81$)				<0.001

[a] See Methods for interpretation of $\underline{P}$ values involving Lek_t and Lek_{t-1}.

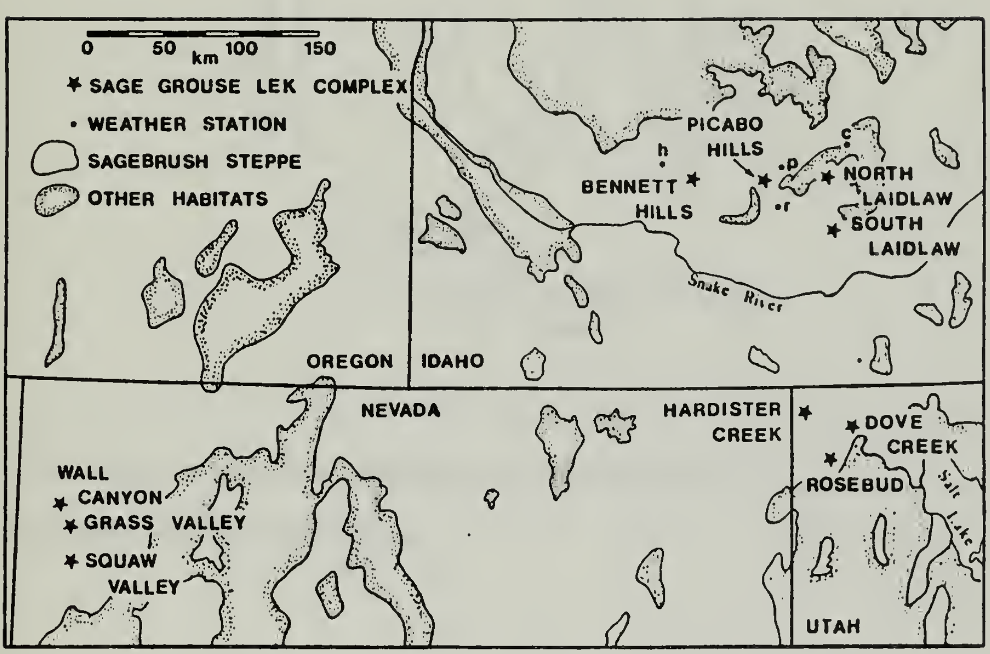

Fig. 1. Map of the Intermountain West showing location of lek complexes, the potential sagebrush steppe habitat (after Küchler 1964), and NOAA weather stations (h = Hill City, p = Picabo, r = Richfield, c = Craters of the Moon).

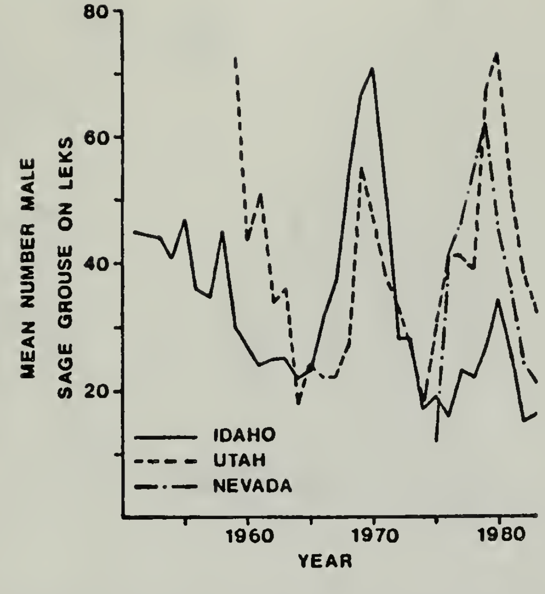

Fig. 2. The mean maximum number of male Sage Grouse per year on subject leks in Idaho, Utah, and Nevada.

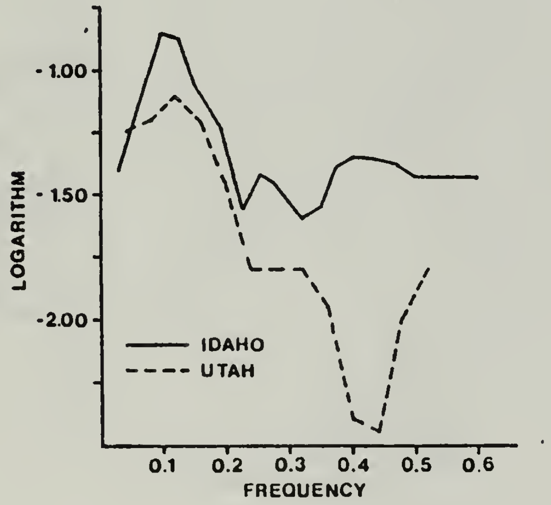

Fig. 3. Spectral analysis of mean lek counts for Idaho and Utah (see text).

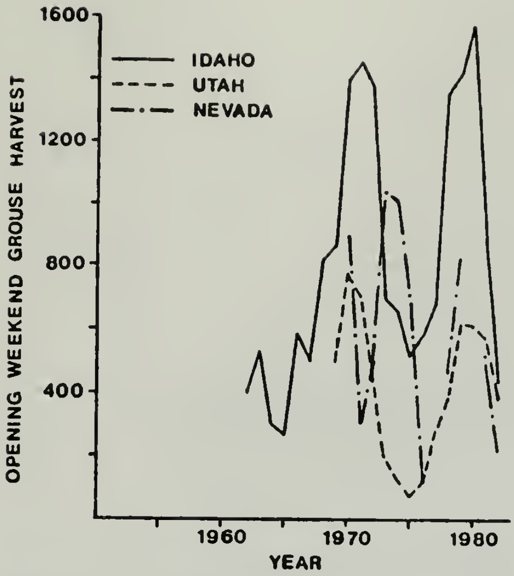

Fig. 4. The yearly harvest of Sage Grouse on the opening weekend of hunting season in Idaho, Utah, and Nevada from geographic regions that correspond with the lek complexes.

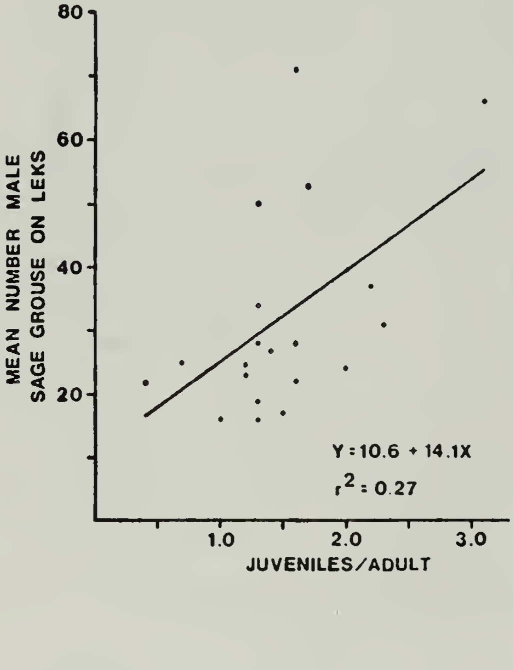

Fig. 5. The relationship between the juvenile/adult ratio of Sage Grouse in the harvest on the opening weekend of hunting season in Idaho and the mean maximum number of males on leks the following spring ($\underline{F} = 6.71$, $\underline{P} < 0.05$).

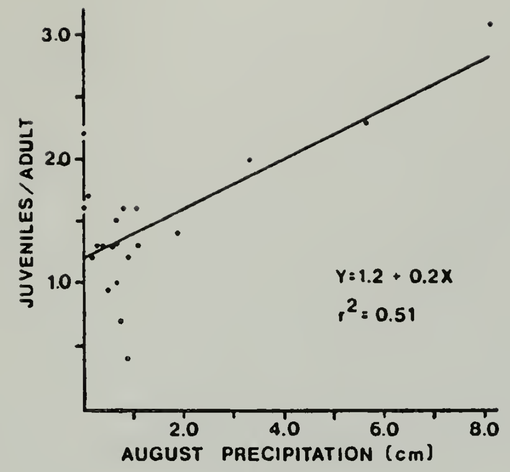

Fig. 6. The relationship between the juvenile/adult ratio in the harvest in Idaho and August precipitation of the same year ($\underline{F}$ = 19.82, $\underline{P} < 0.001$).

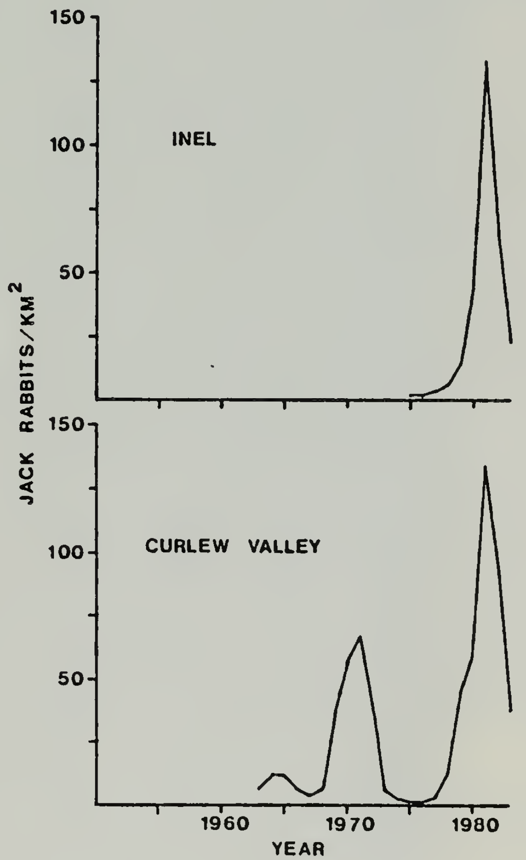

Fig. 7. Spring black-tailed jackrabbit densities in the Curlew Valley of northern Utah and Idaho National Engineering Laboratory (INEL) of southern Idaho (L. C. Stoddart, unpubl.).